Focal Symposium: *Connecting the Threads*
Network Theory for Living Systems

11 November 2010
3:30-7:00 p.m.
Hörsaal 1, UZA 1
Biozentrum
Althanstrasse 14, Wien IX.

David McDonald   *University of Wyoming*

Daniel Rubenstein   *Princeton University*

Michelle Girvan   *University of Maryland*

Ricard Solé   *Universitat Pompeu Fabra, Barcelona*

Steve Phelps   *University of Essex*

Program

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Networks exist at all levels of biological organization, from genes and proteins that interact through mutual regulation over interacting individuals of a population to interacting species in ecosystems. The study of networks and their properties has, therefore, been a rapidly growing field in different biological disciplines—from genetics, via population biology and behavioral ecology to evolutionary biology and ecology (May 2006). At the same time, network models started to play important roles for technical applications, computer networks, and also for the study of human social networks. Research in some of these areas was inspired by developments in other fields, but partly theory and methods were developed in parallel. In this symposium we aim to connect these different threads of scientific inquiry, and to ask how graph theory and network thinking can contribute to our understanding of biological systems.

In population genetics early models of evolutionary processes were based on simplifying assumptions of idealized well-mixed populations. For simplicity it was assumed that all individuals were equally likely to interact and reproduce with each other. The resulting models of evolutionary dynamics, such as the Fisher-Wright process or the Moran process, were very educative and indispensable for our understanding of evolutionary processes. Yet, as natural populations do not comply with these assumptions, a next generation of models, like the island or the stepping stone model, incorporated aspects of population structure. More recently, population ecologists have turned to a different approach and model populations as graphs, which allows one to study *any* possible population structure within a single framework (Proulx et al. 2005). In particular, graph based models have become the first choice to study the effects of spatial structure on evolutionary processes (Lieberman et al. 2005; Ohtsuki et al. 2006; Lehmann et al. 2007; Taylor et al. 2007). Additionally, extensive studies of evolution on simple graphs such as cycles helped to gain deeper insights into general mechanisms of selection processes (Ohtsuki and Nowak 2006; Grafen 2007).

In parallel to the developments in evolutionary biology and population genetics, behavioral ecologists have picked up graphs as their method of choice to represent social groups of animals. This approach started in the 1970's (Wilson 1975) but gained new momentum by influential work in the social sciences (Watts and Strogatz 1998). Again, the idea is to represent social groups as graphs, where vertices correspond to individuals and edges to the social relationships between those individuals. Such, graph representations of social units allow analyses of animal sociality that were impossible with conventional individual-focused approaches (Krause et al. 2007; Croft et al. 2008; Whitehead 2008).

In ecology, network thinking has a considerable tradition, as already some of the founding fathers of modern ecology used network representations and terminology to describe trophic networks or "food webs" (Lindenman 1942; Odum 1956). One of the early tentative conjectures in ecology was that complex ecosystems are more stable, in the sense that those with a richer network of interactions among them were less vulnerable to disturbances (Elton 1958). Ecologists have, therefore, started to assess how the removal of species or their replacement by introduced invaders can alter the trophic network structure (Solé and Montoya 2001; Dunne et al. 2002; Krause et al. 2003). Studies on other kinds of species interactions, such as those between plants and their animal pollinators and seed dispersers, have also benefited from the network approach (Bascompte 2003). Networks turned out to be a useful tool to tackle full communities of pollination mutualisms, and to study how conglomerates of species, rather than only pairs of species, co-evolve (Bascompte et al. 2003).

The first networks at the molecular level were described over 50 years ago by Donald Nicholson (Proulx et al. 2005). With the development of fast and highly efficient molecular methods researchers can now characterize complete protein–protein interaction networks (Uetz et al. 2000) and gene regulatory networks (Lee et al. 2002; Tong et al. 2004). One of the most striking findings in this area is the conservation of network features over millions of years. In a comparison of protein interaction networks across yeast, nematods, and insects, a study by Sharan and colleagues (2005) found that many of the local structures within molecular networks have been conserved over most of evolutionary time. Furthermore, recent studies demonstrated that the position of proteins within a network has important evolutionary consequences. Highly connected proteins in the protein interaction network are more likely to be essential for survival (Jeong et al. 2001), evolve more slowly (Fraser et al. 2002) and are less likely to be lost over evolutionary time (Krylov et al. 2003).

As with any other new methodological framework, the question is to what extent we are making real progress in understanding biological and evolutionary processes or whether we are just telling the same stories with fancy new words (Bascompte 2007). Obviously, network approaches can help us to focus on aspects of population structure that cannot be inferred from observing single individual or dyadic interactions alone. However, the question that remains to be answered is: why are such higher level characteristics of population structures interesting? Despite the growing number of recent network studies, we are—according to Proulx and colleagues (2005)—still in the descriptive 'natural history' phase of this field, discovering the basic structure of biological networks at a variety of scales. In the next phase empirical studies have to provide the motivating details for novel, concept-driven theory and theoretical work must provide a rigorous predictive framework specifically tailored for an evolutionary setting in order to test hypotheses about network formation and network function. In other words, the challenges for the future are to understand (1) how evolutionary forces shape network structure, and (2) how network structure affects evolutionary processes.

References

Bascompte J (2007) Networks in ecology. Basic and Applied Ecology 8:485-490.

Bascompte J, Jordano P, Melian CJ, Olesen JM (2003) The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Science of the USA 100:9383-9387.

Croft DP, James R, Krause J (2008) Exploring Animal Social Networks. Princeton University Press.

Dunne JA, Williams RJ, Martinez ND (2002) Food-web structure and network theory: The role of connectance and size. Proceedings of the National Academy of Science of the USA 99:12917-12922.

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen.

Fraser HB, Hirsh AE, Steinmetz LM, Scharfe C, Feldman MW (2002) Evolutionary rate in the protein interaction network. Science 296:750-752.

Grafen A (2007) An inclusive fitness analysis of altruism on a cyclical network. Journal of Evolutionary Biology 20:2278-2283.

Jeong H, Mason SP, Barabasi AL, Oltvai ZN (2001) Lethality and centrality in protein networks. Nature 411:41-42.

Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW (2003) Compartments revealed in food-web structure. Nature 426:282-285.

Krause J, Croft DP, James R (2007) Social network theory in the behavioural sciences: potential applications. Behavioural Ecology and Sociobiology 62:15-27.

Krylov DM, Wolf YI, Rogozin IB, Koonin EV (2003) Gene loss, protein sequence divergence, gene dispensability, expression level, and interactivity are correlated in eukaryotic evolution. Genome Research 13:2229-2235.

Lee TI, et al. (2002) Transcriptional regulatory networks in *Saccharomyces cerevisiae*. Science 298:799-804.

Lehmann L, Keller L, Sumpter JT (2007) The evolution of helping and harming on graphs: the return of the inclusive fitness effect. Journal of Evolutionary Biology 20:2284-2295.

Lieberman E, Hauert C, Nowak MA (2005) Evolutionary dynamics on graphs. Nature 433:312-316.

Lindenman RL (1942) The trophic-dynamic aspect of ecology. Ecology 23:399-418.

May RM (2006) Network structure and the biology of populations. Trends in Ecology and Evolution 21:394-399.

Odum HT (1956) Primary production in flowing waters. Limnology and Oceanography 1:102-117.

Ohtsuki H, Hauert C, Lieberman E, Nowak MA (2006) A simple rule for the evolution of cooperation on graphs and social networks. Nature 441:502-505.

Ohtsuki H, Nowak MA (2006) Evolutionary games on cycles. Proceedings of Biological Science 273:2249-2256.

Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution. Trends in Ecology and Evolution 20:345-353.

Sharan R, et al. (2005) Conserved patterns of protein interaction in multiple species. Proceedings of the National Academy of Science of the USA 102:1974-1979.

Solé RV, Montoya JM (2001) Complexity and fragility in ecological networks. Proceedings of Biological Science 268:2039-2045.

Taylor PD, Day T, Wild G (2007) Evolution of cooperation in a finite homogenous graph. Nature 447:469-472.

Tong AH, et al. (2004) Global mapping of the yeast genetic interaction network. Science 303:808-813.

Uetz P, et al. (2000) A comprehensive analysis of protein-protein interactions in Saccharomyces cerevisiae. Nature 403:623-627.

Watts DJ, Strogatz SH (1998) Collective dynamics of 'small-world' networks. Nature 393:440-442.

Whitehead H (2008) Analyzing Animal Societies. The University of Chicago Press.

Wilson EO (1975) Sociobiology: The New Synthesis. Harvard University Press.

Connecting the Threads
Network Theory for Living Systems

Schedule

3:30 p.m.   *Opening*
              Gerd B. Müller, Chairman, KLI

3:35 p.m.   *Social Networks: Linking Form with Function in Animal Societies*
              Daniel Rubenstein

4:05 p.m.   *Social Networks in a Lek: Viscosity, Reputation, and Male-Male Cooperation*
              David McDonald

4:35 p.m.   *Emergence of Social Networks from Cooperative Interactions*
              Steve Phelps

5:05 p.m.   Coffee break

5:20 p.m.   *Modeling the Dynamics of Gene Networks*
              Michelle Girvan

5:50 p.m.   *Evolvability, Tinkering, and Causality in Biological Networks*
              Ricard Solé

6:20 p.m.   *Round table discussion among the speakers*
              Werner Callebaut, Moderator

6:40 p.m.   *Open discussion*

7:00 p.m.   *End*

Daniel Rubenstein

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Social Networks: Linking Form with Function in Animal Societies

Animal societies develop from interactions and relationships that occur among individuals within populations. The fundamental tenet of behavioral ecology is that ecological factors shape behavior and determine the distribution and associations of individuals on landscapes. As a result, different social organizations emerge in different habitats and under different environmental conditions. Since characterizations of social systems depend on time and motion studies of individual actions and interactions that are bilateral, they are often coarse-grained. If social relationships are characterized using social networks, however, seemingly similar organizations often differ in terms of deep structure. Thus social network theory should provide insights into the connections between social form and function. Doing so will require a better understanding of how different networks—directed and undirected, passive, agonistic and affiliative, as well as aggregate and dynamic—within populations are related to each other and shape individual 'social personality.' This talk will explore the nature of personality of individuals sharing multiple networks, the link between personality and leadership, especially in altruistic situations, and how the removal or addition of individuals with different personalities affects the spread of memes, genes or disease vectors.

Biographical note

Prof. Daniel Rubenstein is chair of the Department of Evolutionary Biology at Princeton University and director of the Program in African Studies. His research focuses on decision making in animals. He studies how an individual's foraging, mating, and social behavior are influenced by its phenotype, by ecological circumstances, and by the actions of other individuals in the population. Much of his research has centered on understanding the social dynamics of horses, zebras, and asses. His latest research focuses on the rules governing animal movements and migration and involves the interaction of 'self-organizing' behavioral movement rules, ecological information, and habitat structure at multiple spatial scales to understand how migratory animal movements respond to human-induced land use change, and how these changes in movement in turn affect population stability.

Selected publications

Jordan LA, Avolio C, Herbert-Read JE, Krause J, Rubenstein DI, Ward AJW (2010) Group structure in a restricted entry system is mediated by both resident and joiner preferences. Behavioral Ecology and Sociobiology 64:1099-1106.

Fischhoff IR, Dushoff J, Sundaresan SR, Cordingley JE, Rubenstein DI (2009) Reproductive status influences group size and persistence of bonds in male plains zebra (*Equus burchelli*). Behavioral Ecology and Sociobiology 63:1035-1043.

Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier M-J, Rubenstein DI (2007) Social relationships and reproductive state influence leadership roles in movements of plains zebra (Equus burchelli). Animal Behaviour 73:825-831.

Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proceedings of the National Academy of Sciences, USA 104:193-197.

Sundaresan SR, Fischhoff IR, Dushoff J, Rubenstein DI (2007) Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. Oecologia, 151:140-149.

Sundaresan SR, Fischhoff IR, Rubenstein DI (2007) Male harassment influences female movements and associations in Grevy's zebra (*Equus grevyi*). Behavioral Ecology 18:860-865.

Weinstock JE et al (2005) Evolution, systematics, and phylogeography of Pleistocene horses in the New World: A molecular perspective. PloS Biology 3: 1373-1379.

Tien JH, Rubenstein DI, Levin SA (2004) A field study on the proximate mechanisms of fish shoaling. Evolutionary Ecology Research 6:555-565.

Saltz D, Rowen M, Rubenstein DI (2000) The effect of space-use patterns of reintroduced Asiatic wild ass on effective population size. Conservation Biology 14:1852-1861.

Krause J, Hoare JD, Krause S, Hemelrijk CK, Rubenstein DI (2000) Leader-ship in fish shoals. Fish and Fisheries 1:82-89.

David McDonald

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Social Networks in a Lek: Viscosity, Reputation, and Male-Male Cooperation

Lek-mating male Long-tailed Manakins, *Chiroxiphia linearis*, develop complex alliances, over 12-20-year lifespans, culminating in cooperative song and dance displays by an alpha and beta pair at each lek. Using social network approaches, I found that the social connectivity of young males predicted their social status five or more years later (PNAS 104: 10910-10914). While young males interact with many males at several leks, older males interact at fewer leks with fewer males, but have highly-weighted ties to those few (creating social viscosity). These ties reflect performance differences among leks that, in turn, determine female choice. Because females choose via hippocampus-based memory of lek sites, not of individual males, regard for the reputation of the site (the lek) enforces orderly queuing by males, even the males at the end of the queues. Neither kinship nor reciprocity drives this unique cooperative courtship. Instead, younger males benefit by helping establish a reputation whose persistence, maintained by female site fidelity, provides them with direct but delayed benefits. The modularity of the system (with leks acting as distinct but interlinked subnetworks) helps drive the evolution of this unusual social system.

Biographical note

David McDonald is a professor in the Department of Zoology and Physiology, University of Wyoming. He studies behavioral and evolutionary ecology, using a combination of social network models, molecular genetic techniques, matrix-based demographic modelling, and detailed behavioral studies of individually-marked individuals. Current projects include the role of the hippocampus in the evolution of cooperative courtship in manakins, conservation genetics of the Wyoming pocket gopher, black-footed ferret demography, and various aspects of the biology of Rosy-finches.

Selected publications

McDonald DB (2009) Young-boy networks without kin clusters in a lek-mating manakin. Behavioral Ecology and Sociobiology 63:1029-1034.

Ryder TB, McDonald DB, Blake JG, Parker PG, Loiselle PA (2008) Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). Proceedings of the Royal Society B 275:1367-1374.

McDonald DB, Parchman TL, Bower MR, Hubert WA, Rahel FJ (2008) An introduced and a native vertebrate hybridize to form a genetic bridge to a second native species. Proceedings of the National Academy of Science of the USA 105:10842-10847.

McDonald DB (2007) Predicting fate from early connectivity in a social network. Proceedings of the National Academy of Science of the USA 104:10910-10914.

Grenier MB, McDonald DB, Buskirk SW (2007) Rapid population growth of a critically endangered carnivore. Science 317:799.

McDonald DB (2003) Microsatellite DNA evidence for gene flow in neotropical lek-mating Long-tailed Manakins. Condor 105:580-586.

McDonald, DB, Clay RP, Brumfield RT, Braun MJ (2001) Sexual selection on plumage and behavior in an avian hybrid zone: experimental tests of male-male interactions. Evolution 55:1443-1451.

McDonald, DB, Fitzpatrick JW, Woolfenden GE (1996) Actuarial senescence and demographic heterogeneity in the Florida scrub jay. Ecology 77:2373-2381.

McDonald DB, Potts WK (1994) Cooperative display and relatedness among males in a lek-mating bird. Science 266:1030-1032.

McDonald DB (1993) Demographic consequences of sexual selection in the long-tailed manakin. Behavioral Ecology 4:297-309.

Steve Phelps

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Emergence of social networks from cooperative interactions

Traditional game-theoretic models of cooperative behavior assume complete mixing: the probability that x interacts with y is the same for all y. In contrast, recent models emphasise the importance of interactions occurring over networks and the resulting effect on cooperative outcomes. Many of these models assume that the process of network formation is exogenous (eg preferential attachment), or alternatively that the network structure is endogenous but explicit: agents have full knowledge of their own edges which they can manipulate strategically. In contrast, in this talk I introduce a model of cooperation in which network structures emerge from the low-level interactions between agents. This model gives rise to networks whose network properties change dynamically over time, which is consistent with longitudinal studies of social networks in human societies.

Biographical note

Steve Phelps is a Lecturer at the Centre for Computational Finance and Economic Agents, University of Essex. His research focuses on the application of agent-based simulation to economic analysis, and encompasses topics crossing several disciplines: finance, economics (game theory, auction theory, mechanism design), and computer-science (multi-agent reinforcement-learning, design of co-evolutionary algorithms, and complex adaptive systems). He has worked as a consultant for a professional-services company delivering web-based auction solutions, and he co-founded two start-up companies: Ripple Software Ltd. which developed econometric analysis tools for power-sellers in the eBay market place, and Victria Ltd, which developed a prototype dark-pool trading platform.

Selected publications

Phelps S, McBurney P, Parsons S (2010) A novel method for strategy acquisition and its application to a double-action market game. IEEE Transactions on Systems, Man, and Cybernetics B 40(3):668-674.

Phelps S, Nevarez G, Howes A (2009) The effect of group size and frequency of encounter on the evolution of cooperation. In Proceedings of the Tenth European Conference on Artificial Life.

Niu J, Cai K, Parsons S, Gerding E, McBurney P, Moyaux T, Phelps S, Shield D (2008) Jcat: A platform for the tac market design competition. In Padgham L, Parkes D, Mueller JP, Parsons S, editors, Proceedings of the Seventh International Conference on Autonomous Agents and Multi-Agent Systems (AAMAS 2008), Estoril, Portugal.

Phelps S, Cai K, McBurney P, Niu J, Parsons S, Sklar E (2008) Auctions, evolution, and multi-agent learning. In Guessoum Z, Tuyls K, Nowe A, Kudenko D, editors, Adaptive Agents and Multi-Agent Systems III, number 4865 in Lecture Notes in Artificial Intelligence, 188–210. Springer, Berlin.

Phelps S, Marcinkiewicz M, Parsons S, McBurney P (2006) A novel method for automatic strategy acquisition in n-player non-zero-sum games. In Nakashima H, Wellman MP, Weiss G, Stone P, editors, Proceedings of the 5th International Joint Conference on Autonomous Agents and Multiagent Systems (AAMAS 2006), 705–712, Hajodate, Japan, May.

Phelps S, Parsons S, McBurney P (2006) An evolutionary game-theoretic comparison of two double-auction market designs. In Faratin P, Rodriguez-Aguílar JA, editors, Agent-Mediated Electronic Commerce VI, 101–114. Springer.

Phelps S, Tamma V, Wooldridge M, Dickinson I (2004) Toward open negotiation. IEEE Internet Computing, 8:70–76.

Phelps S, Parsons S, Sklar E, McBurney P. Applying genetic programming to economic mechanism design: Evolving a pricing rule for a continuous double auction. In Rosenschein JS, Sandholm T, Wooldridge M, Yokoo M, editors, Proceedings of the Second International Joint Conference on Autonomous Agents and Multi-Agent Systems (AAMAS-2003), 1096–1097, Melbourne, Australia.

Phelps S, Parsons S, Sklar E, McBurney P. Using genetic programming to optimise pricing rules for a double auction market. In Proceedings of the workshop on Agents for Electronic Commerce, Pitsburgh, PA.

Michelle Girvan

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Modeling the Dynamics of Gene Networks

The complex process of genetic control relies upon an elaborate network of interactions between genes. Our goal is to use simple mathematical models to understand the role of network structure in gene regulation. Here, we focus on Boolean systems, which have received extensive attention as useful models for genetic control. An important aspect of Boolean network models is the stability of their dynamics in response to small perturbations. Previous approaches to stability have assumed uncorrelated random network structure. Real gene networks typically have nontrivial topology significantly different from the random network paradigm. To address such situations, we present a general method for determining the stability of large networks of any specified network topology and predicting their steady-state behavior in response to small perturbations. Additionally, we generalize to the case where individual genes have a distribution of 'expression biases,' and we consider a non-synchronous update, as well as extension of our method to non-Boolean models in which there are more than two possible gene states. We find that stability is governed by the maximum eigenvalue of a modified adjacency matrix, and we test this result by comparison with numerical simulations. We also discuss the possible application of our work to experimentally inferred gene networks, and propose that a dynamical instability in the gene regulatory network may be a causal mechanism associated with some cancers.

Biographical note

Michelle Girvan is an Assistant Professor in the Department of Physics and the Institute for Physical Science and Technology at the University of Maryland. Her research focuses on the application of network theory to biological and social systems. She has worked extensively on finding and evaluating modular structures in large complex networks. More recently, she has been exploring the role of network structure in gene regulation.

Selected publications

Pomerance A, Ott E, Girvan M, Losert W (2009) The effect of network topology on the stability of discrete state models of genetic control. Proceedings of the National Academy of Science of the USA 106:8209-8214.

Ott E, Platig JH, Antonsen TM, Girvan, M. (2008): Echo phenomena in large systems of coupled oscillators. Chaos 18:037115.

Flack JC, Girvan M, deWaal F, Krakauer D (2006) Policing Stabilizes the Construction of Social Niches in Social Primates. Nature 439:426-429.

Wiley D, Strogatz SH, Girvan M (2006) The size of the sync basin. Chaos 16:015103.

M. E. J. Newman and M. Girvan (2004) Finding and evaluating community structure in networks. Physical Review E 69:026113.

Girvan M, Newman MEJ (2002) Community structure in social and biological networks. Proceedings of the National Academy of Science of the USA 99:8271-8276.

Girvan M, Callaway DS, Newman MEJ, Strogatz SH (2002) A simple model of epidemics with pathogen mutation. Physical Review E 65:031915.

Ricard Solé

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Evolvability, Tinkering, and Causality in biological networks

The study of complex systems, particularly biological ones, in terms of networks of connected units has been shown to reveal some unexpected features of these systems. By looking at the modular organization of protein maps at different levels and comparing them with null models of graph growth with no functionality, it can be shown that a large part of their structural organization can be understood as a byproduct of the duplication-rewiring rules. In other words, tinkering is able by itself to produce small world, scale-free and modular networks without considering fine-tuned selective pressures. In this context, some of the observed regularities might actually correspond to evolutionary spandrels. Finally, we also give a look to technological networks, finding evidence of tinkering in spite of their obviously designed nature.

Biographical note

Ricard Solé is ICREA research professor (the Catalan Institute for research and Advanced Studies) and Head of the Complex Systems Lab at the Universitat Pompeu Fabra. Since 1997, he has been an external professor of the Santa Fe Institute (New Mexico, USA). His main research interest is understanding the possible presence of universal patterns of organization in complex systems, from prebiotic replicators to evolved artificial objects. Key questions are how robust structures develop, how information is incorporated into these structures and how computation emerges. He investigates principles of organization responsible for the emergence of fundamental components of complexity, including the origins of self-reproduction, development, life cycles, computational processes, and multicellularity.

Selected publications

Solé RV (2010) Phase transitions: from genes to ants and social collapse. Princeton University Press.

Joppa L, Montoya JM, Solé RV, Sanderson J, Pimm S (2010) On nestedness in ecological networks. Evolutionary Ecology Research 12:35-46.

Mestres J, Gregori-Puigjané E, Valverde S, Solé RV (2008) Data Completeness: the Achilles heel of Drug-Target Networks. Nature Biotechnology 26:983-984.

Solé RV (2007) Scaling laws in the drier. Nature 449:151-153.

Montoya JM, Pimm S, Solé RV (2006) Ecological networks and their fragility. Nature 442:259-264.

Solé RV, Bascompte J (2006) Self-organization in complex ecosystems. Monographs in Population Biology, Princeton University Press, 325-344.

Solé RV (2005) Syntax for free? Nature 434:289.

Montoya JM, Solé RV (2003) Topological properties of food webs: from real data to community assembly models. Oikos 102:614-622.

González-García I, Solé RV, Costa J (2002) Common Pattern Formation, Modularity and Phase Transitions in a Gene Metapopulation dynamics and spatial heterogeneity in cancer. Proceedings of the National Academy of Sciences USA 99:13085-13089.

Montoya JM, Solé RV (2002) Small World Patterns in Food Webs. Journal of Theoretical Biology 214, 405-412 (2002)

Theraulaz G, et al (2002) Spatial Patterns in Ant Colonies. Proceedings of the National Academy of Sciences of the USA 99:9645-9649.

Solé RV, Salazar-Ciudad I, Newman SA (2000) Gene network dynamics and the evolution of development. Trends in Ecology and Evolution 15:479-480.